Nature Conservation

Nature Conservation 58: 243–260 (2025)
DOI: 10.3897/natureconservation.58.142210

Research Article

Establishing priorities for future land conservation to maximise biodiversity conservation and other ecosystem services in the Tilarán Mountains of Costa Rica

Lindsay Stallcup[1], Matthew D. Moran[1], Doris Rojas[1], Erich Mata[1]

1 Monteverde Conservation League, Children's Eternal Rainforest, Monteverde, Puntarenas, Costa Rica
Corresponding author: Matthew D. Moran (moran@hendrix.edu)

Abstract

The Monteverde-Arenal Bioregion (MAB), located in the Tilarán Mountains of north-central Costa Rica, contains some of the most biodiverse habitats in Costa Rica and also provides the backbone for some of Costa Rica's most important ecotourism destinations. Several national parks and private preserves protect a large area of habitat in the region, but this complex of protected areas is isolated from other large protected areas because of deforestation associated mostly with agricultural development, plus a smaller amount of urban development. Furthermore, we are aware of no detailed analysis to identify landscapes in need of protection in order to secure the conservation of the region's biodiversity into the future. Using GIS technology, we analysed select conservation-related ecosystem services in order to identify the lands of highest future conservation priority outside of existing protected areas in the MAB. We identified large areas of habitat on the Pacific slope to the south and west of the existing protected areas and habitat adjacent to Lake Arenal to the northwest of existing protected areas as having the highest ecosystem services values. In contrast, most lands on the Caribbean slope outside of the existing protected areas had comparatively lower ecosystem services values. Based on this analysis, we recommend that future conservation efforts, including potential land purchase, should focus on conserving mid-elevation Pacific slope forests and land along previously proposed biological sub-corridors that could connect the MAB to other existing protected areas. Our analysis shows that many important landscapes for biodiversity conservation in and near the MAB currently exist outside of protected areas, making many species found in those areas vulnerable to human activities. The opportunity to connect currently protected areas to one another through effective biological corridors still remains, possibly through conservation partnerships with landowners or direct land purchase, but time could be short as increasing development and changing land-use patterns threaten to further isolate habitats in the MAB.

Key words: Biological corridors, Costa Rica, GIS, land-use, Mesoamerica, Tilarán Mountains, tropical forest

OPEN ACCESS

Academic editor: João Pompeu
Received: 19 November 2024
Accepted: 8 February 2025
Published: 30 April 2025

ZooBank: https://zoobank.org/1D34FA5C-A9FF-4F48-BEC9-45729CD80C74

Citation: Stallcup L, Moran MD, Rojas D, Mata E (2025) Establishing priorities for future land conservation to maximise biodiversity conservation and other ecosystem services in the Tilarán Mountains of Costa Rica. Nature Conservation 58: 243–260. https://doi.org/10.3897/natureconservation.58.142210

Introduction

The Monteverde-Arenal Bioregion (MAB), located in the Tilarán Mountains of Costa Rica, has some of the highest biodiversity in Central America and simultaneously represents one of the most important ecotourism destinations of the

country (Aylward et al. 1996; Langholz et al. 2000; Koens et al. 2009; Stuckey et al. 2014). The area has several important public and private protected areas, the most important amongst them being the privately owned Children's Eternal Rainforest (22,600 hectares) and Monteverde Cloud Forest Reserve (4,125 hectares) and the state-owned Arenal Volcano National Park (12,124 hectares), Alberto Manuel Brenes Biological Reserve (7,800 hectares) and Santa Elena Cloud Forest Reserve (310 hectares). Along with a number of smaller, mostly privately owned protected areas, the total area in conservation in our study area is about 50,000 hectares, including protected habitat in eight Holdridge life zones (Holdridge 1947, 1967; five regular + three transitional zones) on both Caribbean and Pacific slopes (Fig. 1).

The region is noted for its high biodiversity, especially for plants, amphibians and birds (Haber 2000; Wheelwright 2014; Newcomer et al. 2022). For example, the Monteverde area (defined as all lands above 700 m a.s.l. in the MAB) alone contains over 450 species of orchids, perhaps the greatest diversity in the world for a single area of similar size (Haber 2000). Numerous endemic species exist here (Newcomer et al. 2022), probably because of the relative isolation of the higher elevation habitats. The region is also home to a number of endangered or threatened species (e.g. Bare-necked Umbrellabird (*Cephalopterus glabricollis*), Baird's tapir (*Tapirus bairdii*)), further solidifying the MAB as an important priority for conservation efforts in Costa Rica and beyond.

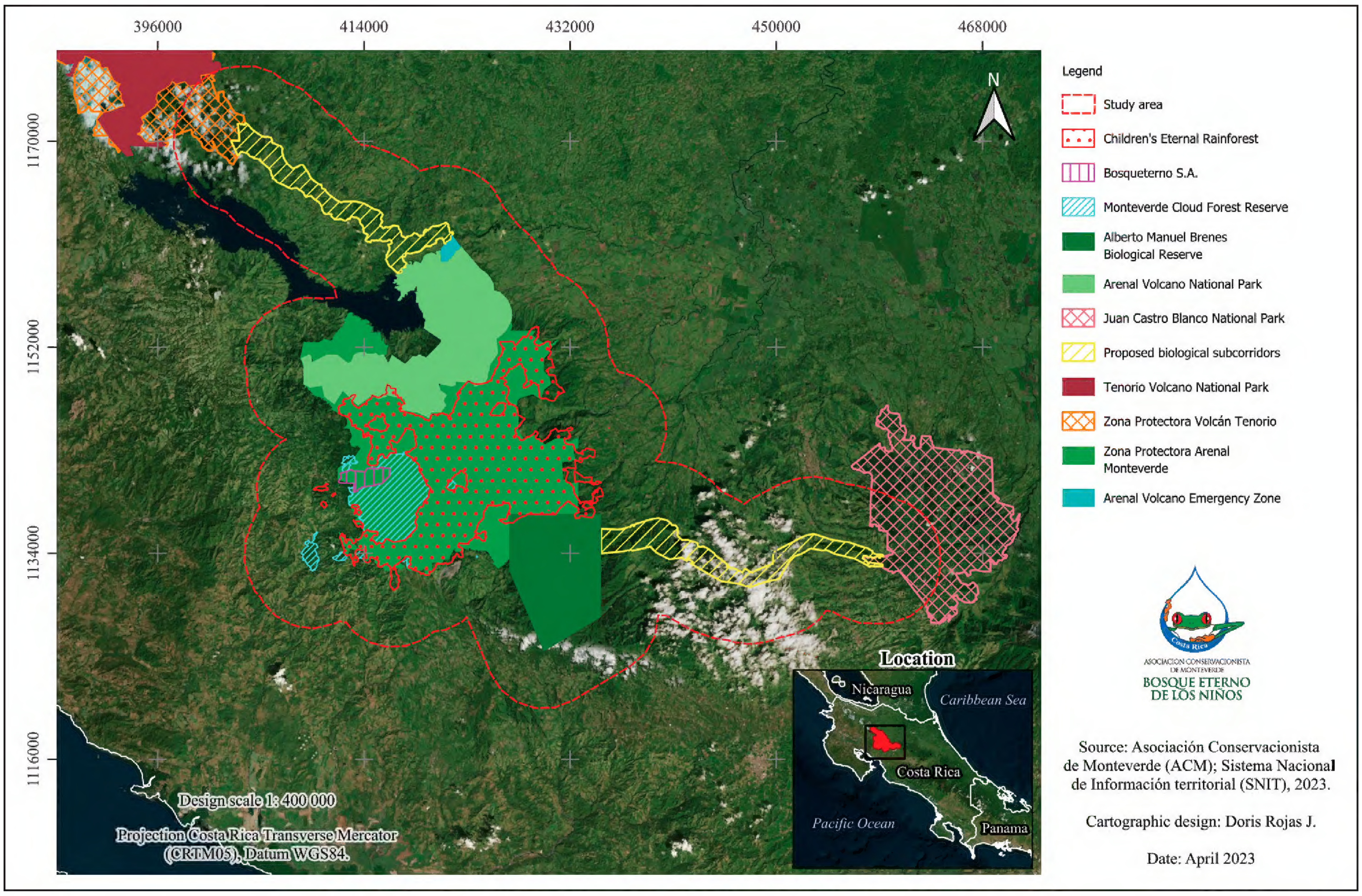

Figure 1. Study area showing boundaries of analysis (red outline), protected areas with ownership designation and proposed biological sub-corridors (in yellow outline) Moran et al. (2019).

The area also is a prime location for ecotourism, with Monteverde and La Fortuna (as well as smaller nearby communities) hosting hundreds of thousands of national and international visitors annually (Koens et al. 2009). These high visitation rates, in turn, support a vibrant tourism economy focused on nature and biodiversity (Aylward et al. 1996; Langholz et al. 2000; Koens et al. 2009; Stuckey et al. 2014). Charismatic avian species such as the Resplendent Quetzal (*Pharomachrus mocinno*) and the Three-wattled Bellbird (*Procnias tricarunculatus*) are major attractions, as are dramatic geological features, such as the Arenal Volcano and associated hot springs. Subsequently, a large proportion of the local human population is involved in tourism and, in general, there is a strong conservation ethic in the local communities where ecotourism thrives (Newcomer et al. 2022).

While conservation efforts in the Monteverde-Arenal Bioregion have been successful, most of the land that has been protected to date is at higher elevations and/or includes steep terrain and is not well suited for traditional land use, such as agriculture. Lower elevations in the region remain mostly unprotected, resulting in an island of conservation in a larger sea of partial deforestation and development (Sánchez-Azofeifa et al. 2003; Moran et al. 2019). As a result, the MAB has lost connectivity with surrounding habitats, perhaps limiting the persistence potential of organisms that require large, connected tracts of habitat (e.g. jaguar, *Panthera onca*). However, studies have shown that this region retains much of its biodiversity, including large mammals that require extensive habitat (Zamzow et al. 2018) and that partially forested, privately owned corridors connecting the Tilarán Mountains to other protected areas do persist (Moran et al. 2019; Beita et al. 2021). As conservation efforts have primarily been focused on higher elevations, lower elevation slopes and their associated life zones (some of which are completely unprotected in our study area) and unique species remain vulnerable to deforestation and other negative impacts.

The MAB is also part of the Mesoamerican Biological Corridor, one of the most diverse ecoregions of the world, representing one of the identified hotspots of biodiversity on Earth. This large corridor connects the distant bioregions of the North and South American continents and is, therefore, of outstanding importance for both animals that need large ranges (e.g. *Panthera onca*) and species that migrate seasonally across the region (e.g. migratory Neotropical birds). Therefore, successful land conservation in this region will further the goals of larger Mesoamerican biodiversity protection (Miller et al. 2001; Harvey et al. 2008; Holland 2012; Jiménez-López et al. 2023).

In this study, we analysed select ecosystem services for landscapes in and around the Monteverde-Arenal Bioregion through the use of geographic information systems (GIS). Our goal was to identify priority lands for future conservation efforts, including direct purchase as well as other conservation initiatives. We hoped that we could identify areas that would be best utilised for conservation, while simultaneously identifying lands that are better left to remain in traditional economic activities, such as agriculture, businesses and other human infrastructure. We also sought to identify suitable potential biological corridors that could connect the MAB to nearby protected areas, as such corridors would represent high priority land for conservation for their ability to reduce regional fragmentation.

Methods

Study region

We studied the area in and around the MAB, located in the Tilarán mountain range of north-central Costa Rica, one of most important protected areas in Central America (Newcomer et al. 2022, Fig. 1). This area is known for its high biodiversity, variety of Holdridge life zones (Fig. 2A, B), geological features, water resources and thriving ecotourism economy. The region is somewhat geographically isolated from other highland areas and, unsurprisingly, endemism rates are high, particularly for plants and amphibians (Haber 2000; Pounds and Fogden 2000; Wheelwright 2000). The MAB has a series of noteworthy reserves and parks, creating a contiguous block of about 50,000 hectares of protected land, as well as several smaller, discontinuous protected areas along the margins (Fig. 1). Lower elevation areas surrounding the MAB remain largely unprotected, meaning that the complex of parks and preserves is essentially an island of forest surrounded by a sea of fragmented habitat (Fig. 2C). However, some partially- to mostly-forested corridors still exist, presumably allowing for dispersal of some organisms northwest into protected areas in the Guanacaste mountain range and southeast

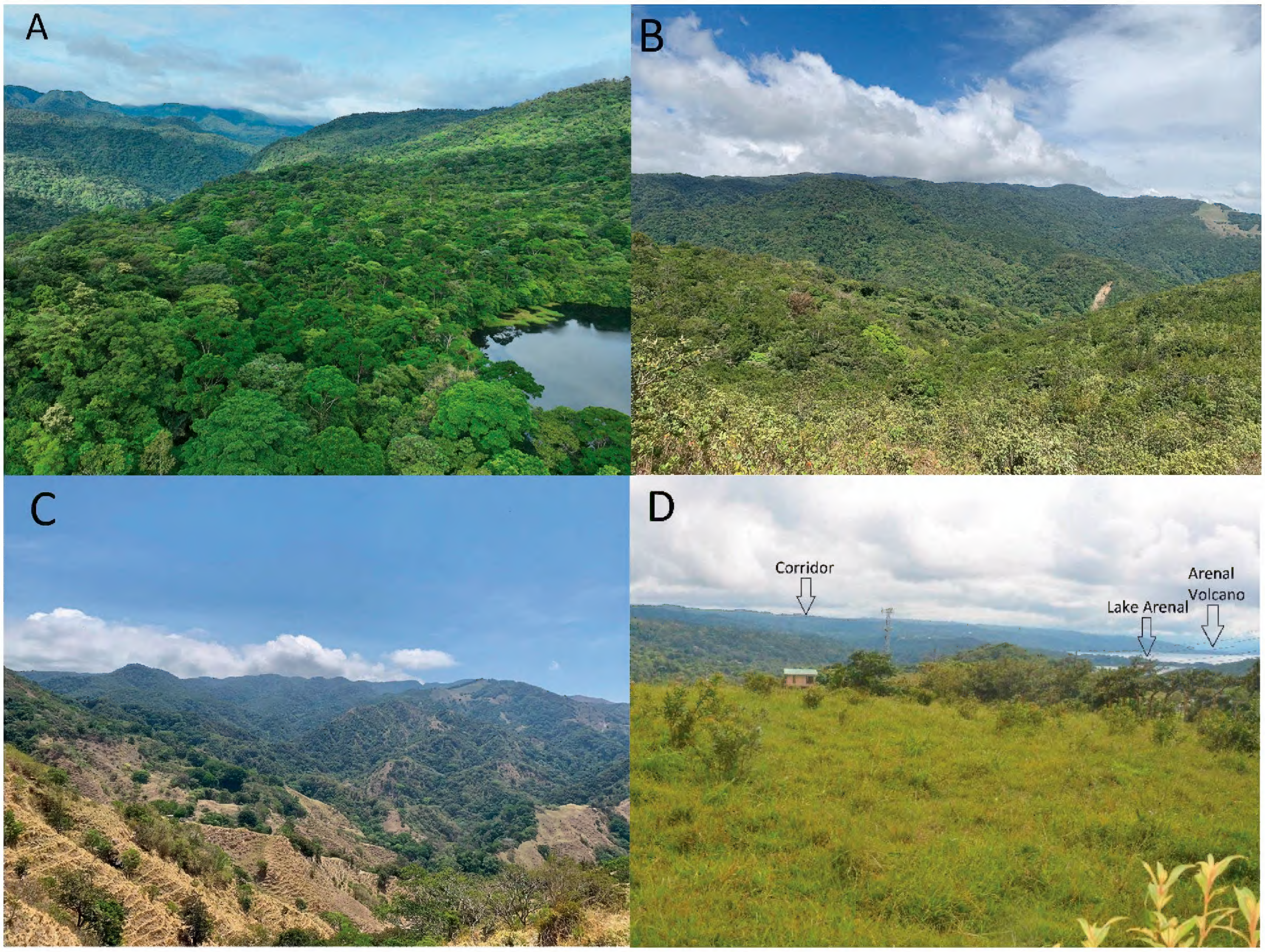

Figure 2. Photographs of landscapes within the study area **A** Peñas Blancas Valley on the Caribbean slope of the MAB area **B** San Luis Valley on the Pacific slope of the MAB; much of this area is secondary forest that has regenerated in the last three decades **C** fragmented habitats lower on the Pacific slope showing heavy deforestation and fragmentation due to agricultural activity **D** partially forested, but largely unprotected corridor (about 2/3rds native forest) between the MAB (Arenal Volcano National Park visible on far right of photo) and Tenorio National Park protected lands.

towards protected areas in the Central Highlands (Moran et al. 2019, Fig. 2D). For instance, after decades of apparent absence, the jaguar (*P. onca*) has recolonised the region's protected areas in small numbers (Zamzow et al. 2018, MDM and LS, personal observations), presumably using such dispersion corridors.

We chose to analyse the landscapes adjacent to protected areas within the MAB, plus areas around the two biological sub-corridors proposed in Moran et al. (2019). We examined all lands within a 5 km radius of the boundaries of existing protected areas and the two proposed sub-corridors (Fig. 1). The north-western and south-eastern limits of the study were the two largest protected areas nearest to the MAB: the complex formed by Tenorio Volcano National Park and the Tenorio Volcano Protected Zone (hereafter, "Tenorio complex") and Juan Castro Blanco National Park, respectively. The total area analysed (i.e. study area) was about 174,000 hectares.

Ecosystem services calculations

While there are numerous ecosystem services for all landscapes (TEEB 2010), we chose six which we suggest are important for the study area and for which there are adequate data available for Costa Rica and for our study area in particular (Table 1). For each of these six ecosystem services, we calculated a relative value for all locations within the study area to indicate each location's conservation priority with respect to that ecosystem service. Each ecosystem service (ES) was weighted equally. We recognise that the decision to weigh all six ES equally is arbitrary and that a great variety of additional models could have been constructed. Spatial data for constructing the maps were obtained from a variety of sources: ES #1 directly from authors of a published paper (Moran et al. 2019), ES #2, 3 and 4 from the National Territorial Information System of Costa Rica (*Sistema Nacional de Información Territorial*, SNIT 2023), ES #5 from biodiversity data from Kohlmann (2011) and applied spatial data from SNIT (2023) and ES#6 from information provided by relevant hydroelectricity producers.

For each ES, we ranked individual locations with a score of 0, 1 or 2, with zero being the lowest priority and 2 being the highest priority (see individual descriptions, below). We recognise that there is a certain level of arbitrariness to this decision; for the quantitative measures, we generally divided the values into 33.3% percentiles. While we have considered these ecosystem services separately,

Table 1. List of selected ecosystem services measured in this study with short descriptions of their value to conservation.

Ecosystem Service	Benefits	Method of Calculation
biological corridors	migration/dispersal of species, genetic connectivity, reduced mortality	arbitrary assignment of value (0, 1 or 2)
protection of land with steep slopes	reduced soil erosion, reduced landslide risk, water quality	assignment of value based on slope angle
land-use/forest cover	carbon sequestration, ecotourism, biodiversity protection, local climate and air quality	assignment of value based on forest, pasture or urban development
life zones	biodiversity	assignment of value based on zone-specific biodiversity, rarity and level of protection
biodiversity	genetic wealth, ecotourism, ecosystem	assignment of value based on endemism and overall species diversity
hydroelectric generation	clean electricity, economic well-being	assignment of value based on watershed-specific power generation

we recognise that some of these ecosystem services interact in complex ways (e.g. steep slopes have both high erosion potential and high hydroelectric generation potential). Conserving the ecosystem services which we studied in this project is also likely to enhance additional services for which we lack data.

Biological corridors and connectivity

We considered the following areas, which would reduce regional habitat fragmentation, to be high priority landscapes for conservation: existing biological corridors as defined by Costa Rica's National System of Conservation Areas (*Sistema Nacional de Areas de Conservación*, SINAC); forested land that would connect existing protected areas in the MAB to nearby protected areas; and private inholdings completely surrounded by existing protected areas. We assigned high conservation priority to the two sub-corridors proposed in Moran et al. (2019). These sub-corridors are located within larger biological corridors as defined by SINAC and would connect the complex of preserves in the MAB to the Tenorio Complex to the northwest and Juan Castro Blanco National Park to the east. We also included the Bellbird Biological Corridor, an existing initiative on the Pacific slope with the objective of improving and conserving ecological connectivity between high elevation cloud forests in the Tilarán mountain range and the mangrove forests along the Gulf of Nicoya (Fig. 1). The Bellbird Biological Corridor spans 11 Holdridge life zones, from 1,800 m a.s.l. to sea level and protects habitats that are important for seasonal altitudinal migrants, including the endangered Three-wattled Bellbirds (*P. tricarunculatus*) and many species of butterflies. We assigned private inholdings within the Children's Eternal Rainforest (at the heart of the MAB) and the two proposed sub-corridors from Moran et al. (2019), a value of 2, land within the Bellbird Biological Corridor a value of 1 and all other land a value of 0.

Slope

We used slope as a proxy for the ecosystem service of soil conservation and erosion prevention. Landslides are also costly to infrastructure and hazards to human life, so preserving forest cover on steeply-sloped land has numerous societal benefits (Kjekstad and Highland 2009; Lehmann et al. 2019). We defined three ranges of slope angle: < 5%, 6 to 35% and > 35% and assigned them values of 0, 1 and 2, respectively.

Land-use

We defined three basic categories of land use: forest, pasture and developed/intensive agriculture (i.e. urban, suburban, other human structures and permanent crops), based on the GIS data available for the study area. Available databases do not differentiate between native forest (defined as both primary and secondary forest) and plantation forests; however, the vast majority of forests in the study area are naturally occurring (Moran et al. 2019; MDM personal observations). We assigned existing forest the highest potential conservation value (2) and developed/intensive agricultural areas the lowest value (0), due to the existing economic value of this land and the low likelihood of its conversion

to natural habitat. While primary forest tends to support the highest biological diversity, in this study, we regard primary and secondary forest as equal conservation value. In this region of Costa Rica, natural reforestation is rapid and tends to support high biodiversity within a short period of time (Janzen and Hallwachs 2020). Pasture lands were assigned a value of 1, since natural reforestation to native habitat is both possible and has commonly occurred in the study area (Chacón-Cascante et al. 2012; Stan and Sanchez-Azofeifa 2019).

Life Zones

We assessed the value of each Holdridge life zone (Holdridge 1947) in our study area, based on a combination of life zone rarity (i.e. the proportion of the total study area for each particular life zone) and degree of current protection (i.e. the proportion of each life zone currently under protection within the study area). We utilised the following formula:

$$\boldsymbol{Life\ Zone\ Priority} = (\boldsymbol{Alz}\ /\ \boldsymbol{At}) * (\boldsymbol{Ap}\ /\ \boldsymbol{Alz})$$

where: A_{lz} = area (hectares) of life zone in the study area, A_t = total study area (hectares) and A_p = area (hectares) of life zone officially protected within the study area.

This formula produced an inverse relationship: lower scores indicate rare and poorly-protected life zones that should be given higher conservation priority, while high scores indicate life zones that are already well-represented within existing protected areas in the study area and, therefore, are of lower conservation priority. Life zones with a score of 0 (i.e. 0% protected) were assigned a value of 2; life zones with a score of 0.01 to 0.05 were assigned a value of 1; and life zones with a score of 0.05 or greater were assigned a value of 0.

Biodiversity

We assigned a numerical value to biodiversity based on two variables, number of endemic species and species richness, of selected groups for which there is reliable country-wide data as calculated by Kohlmann (2011). These groups included two taxonomic groups of insects (Scarabaeinae, Dynastinae), three plant families (Araceae, Arecaceae, Bromeliaceae) and fish (Osteichthyes). While these select taxonomic groups are not an exact measure of biodiversity (and fish are species-poor in the study area), the unfortunate paucity of specific biodiversity data for many tropical ecosystems and for our study area in particular, precluded an exact measure of total biodiversity. However, plant diversity is often a suitable proxy for total biodiversity (Brunbjerg et al. 2018) and the protection of endemic species is a particularly high priority for conservation (Cañadas et al. 2014).

The number of species + the number of endemics was summed and these values divided into 33.3% percentiles, then assigned values on the 0–2 scale used in the other ecosystem services measured. One Holdridge Life Zone lacked biodiversity data (Bosque Pluvial Montano Bajo), so it should be noted that this life zone had a lower potential total conservation value in the final calculation as compared to the others.

Hydroelectric generation

Costa Rica has a largely carbon-free electricity grid (Teske et al. 2020) and the majority of the country's electricity comes from hydroelectric generation. We assumed that forested land in watersheds with hydroelectric projects is of greater value with respect to the ecosystem service of electricity generation than forested land in watersheds without hydroelectric facilities (Chang 2006). We divided our study area into sub-watersheds and acquired hydroelectric generation data (MWh per year) for the six hydroelectric projects located within the study area. We then divided the total annual generation (MWh) of each hydroelectric project by the total number of hectares in the catchment upstream of the hydroelectric project. The end result was a range of 0–17.84 MWh/hectare for each watershed (some watersheds have more than one hydroelectric project). Watersheds with a value of 15.0 or greater were assigned a score of 2; watersheds with a value of 5.0–14.9 were assigned a score of 1 and watersheds with a value < 5.0 were assigned a score of 0.

Final formula

The values from the six ES categories were totalled to produce a total priority score, with a minimum – maximum range from 0 to 12. These values were then plotted on to a "heat map" of the study area to show land with the highest combined ranking of ecosystem services and that should, therefore, be considered of highest conservation value for future conservation action.

Results

The MAB has large altitudinal gradients over a relatively small geographical area, resulting in many steeply-sloped lands (Figs 2A, B, 3). Most of the existing protected areas occur at higher elevations and in areas of steep slopes. Outside of the existing protected areas in our study area, the Pacific slope to the south and west has large areas of steeply-sloped landscapes (Fig. 2C), while land to the north and east of the existing protected areas is comparatively flat. The proposed sub-corridor connecting the MAB region to Juan Castro Blanco National Park has smaller areas of steeply-sloped lands, primarily in the major river valleys.

Land use in the study area is highly correlated with land already under some measure of conservation or protection. Unsurprisingly, protected areas are almost entirely covered in tropical forest (of various life zones), which is the natural land cover of the entire region (Fig. 4). There are large patches of forest located to the south and east of the existing protected areas, especially in and around the proposed sub-corridor connecting the MAB to Juan Castro Blanco National Park. Smaller forested areas exist on the Pacific slope to the southwest of existing protected areas and there are other small patches of forest in the proposed sub-corridor connecting the MAB to Tenorio National Park to the northeast. Most non-forested land in the study area is pasture land devoted to cattle ranching (both dairy and beef, MDM personal observations), although substantial areas to the northeast of the main protected areas have cultivated crops (these areas also correspond to the lands with more gentle slopes, Fig. 3).

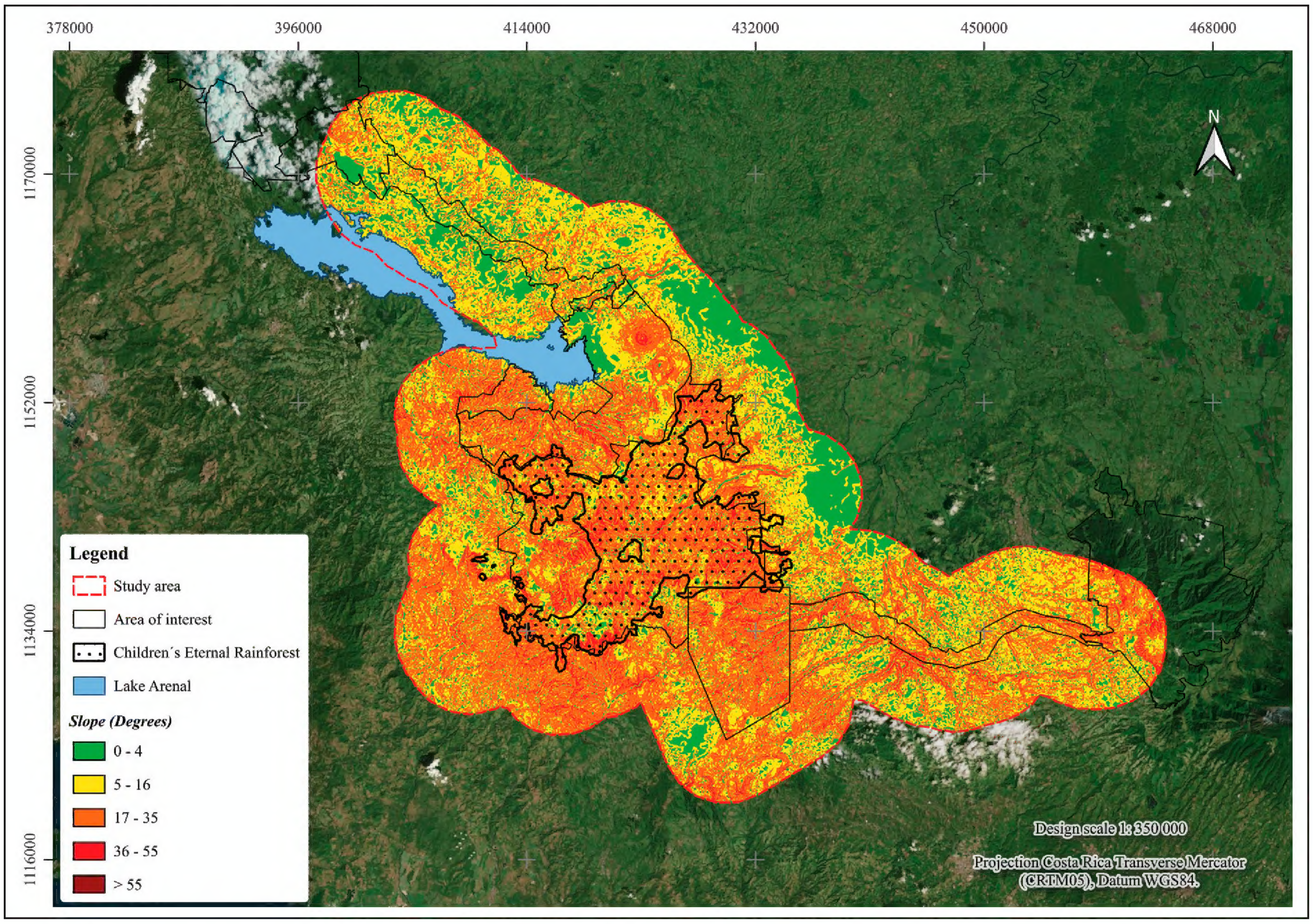

Figure 3. Slope angle within study area.

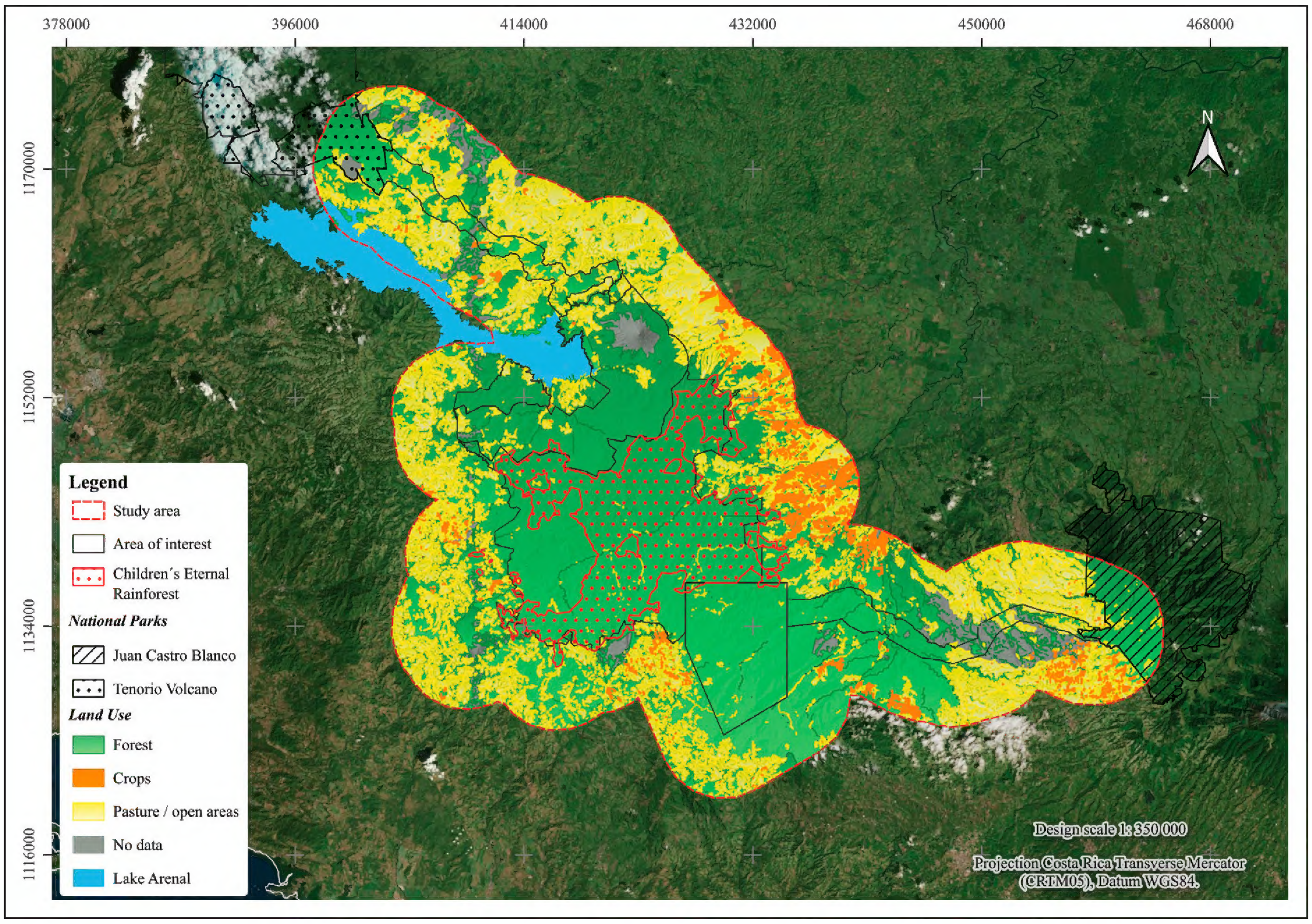

Figure 4. Land-use within the study area.

The study area spans 11 Holdridge life zones. Most of the protected areas of the MAB fall within the lower montane rainforest and premontane rainforest life zones, with smaller areas of tropical wet forest transition to premontane (Fig. 5). The other eight life zones present in the study area are poorly protected and three are completely unprotected. Most notably, on the Pacific slope to the south and west of the existing protected areas, there is a series of closely altitudinally-spaced life zones that fall almost entirely outside of protected areas and also have high biodiversity values (Fig. 6) and some intact forest (Fig. 2C). Conversely, many lower elevational Caribbean slope life zones are also unprotected in their entirety within the study area, but are also almost totally cleared of native vegetation due to agricultural activity (Fig. 4).

There are six major hydroelectric projects within the study area: one on the Pacific slope and five on the Caribbean slope (Fig. 7), the area that receives the most rain (Waylen et al. 1996). The Arenal facility is the most important generation facility in the study area, producing about 30% of Costa Rica's total hydropower. In total, more than 1 million MWh are produced annually from water provided by protected areas of the MAB, about 10% of Costa Rica's total electricity production and about 13% of its hydroelectric power generation (Our World of Data 2023), even though it represents less than 5% of the country's terrestrial area.

When we combine all of the selected ecosystem services, the areas that should be given highest priority for conservation are generally located in two distinct locations: land on the Pacific slope to the south and west of the existing

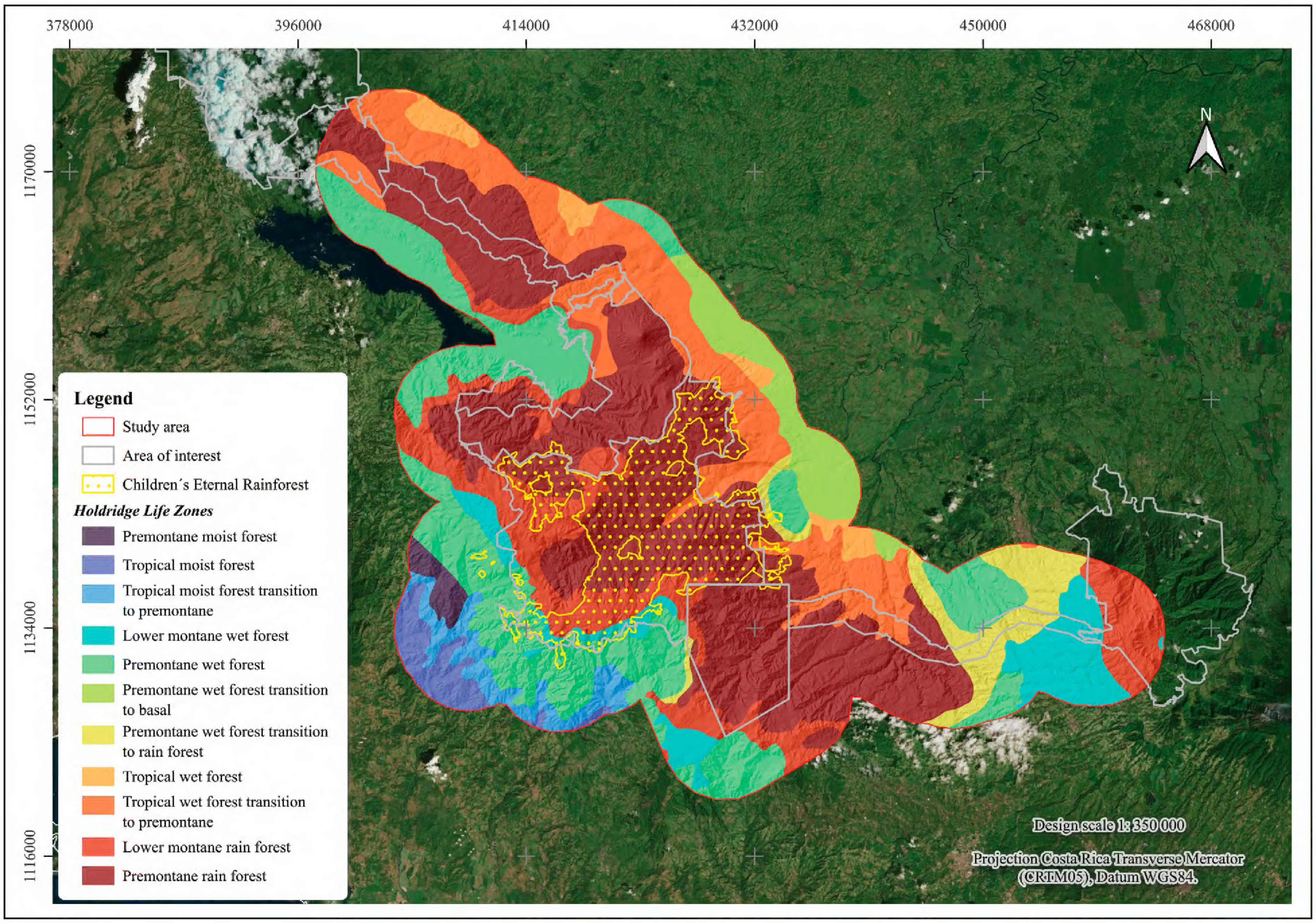

Figure 5. Holdridge life zones within the study area.

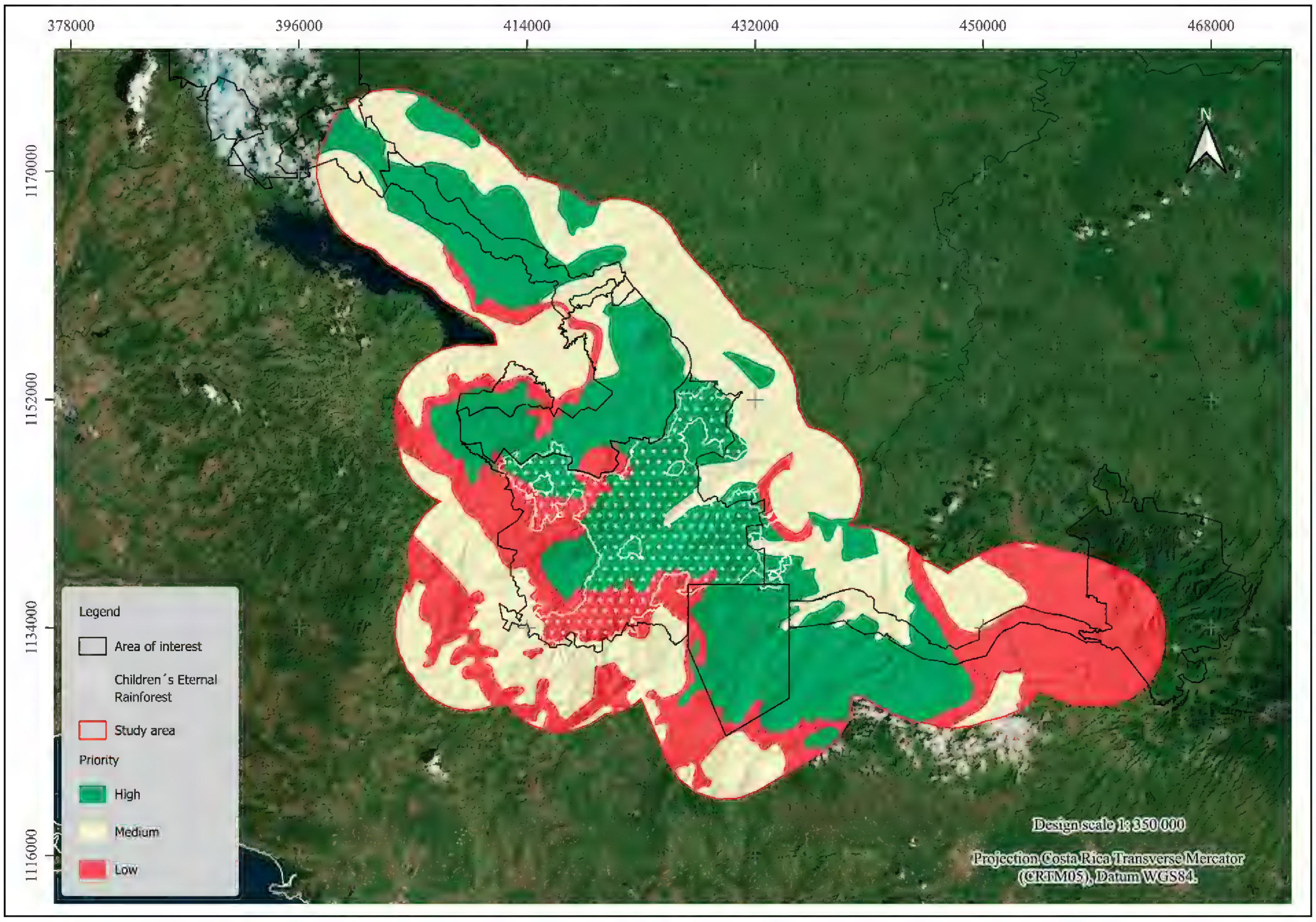

Figure 6. Life zone-specific biodiversity rankings within the study area.

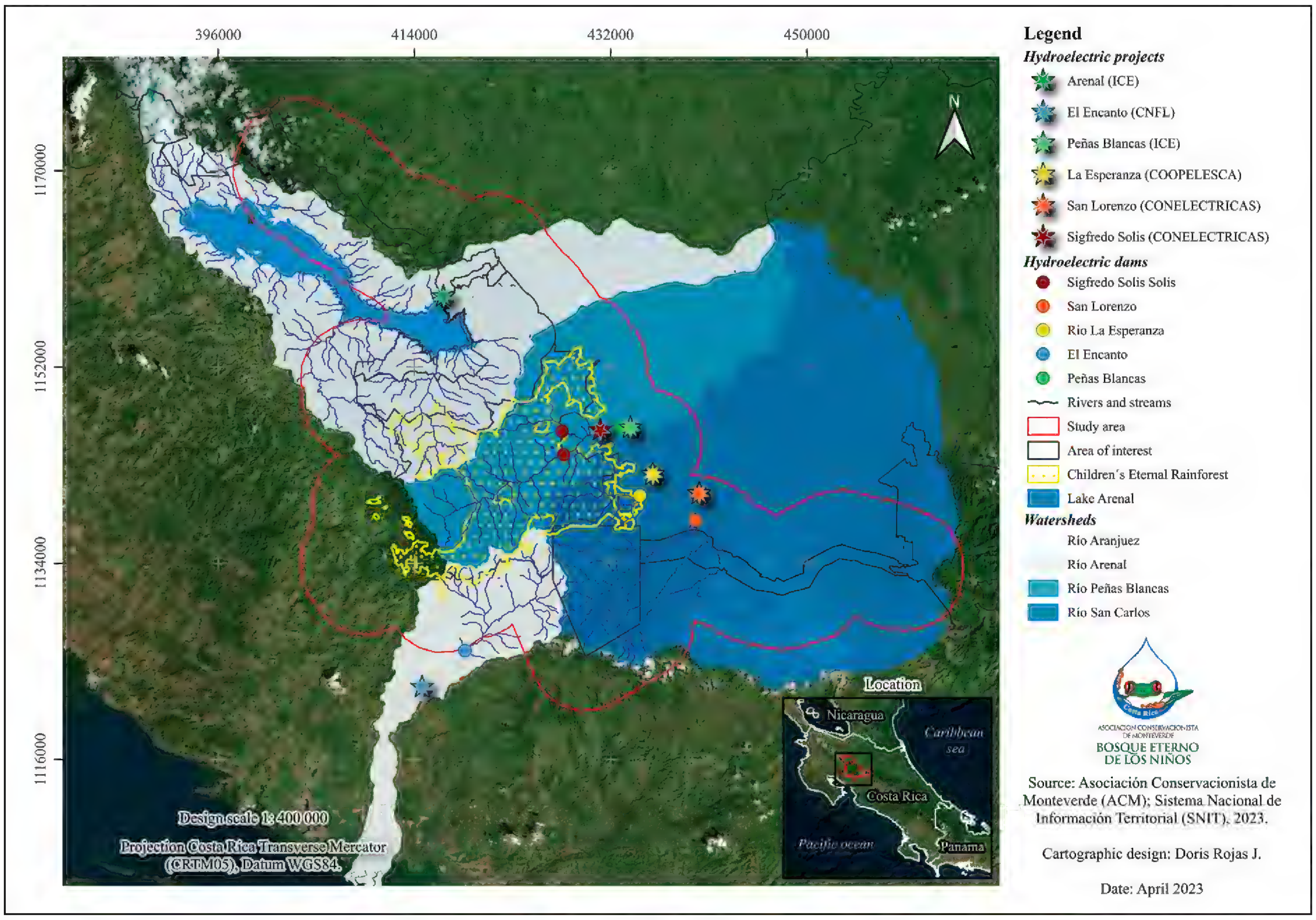

Figure 7. Hydroelectric resources within the study area.

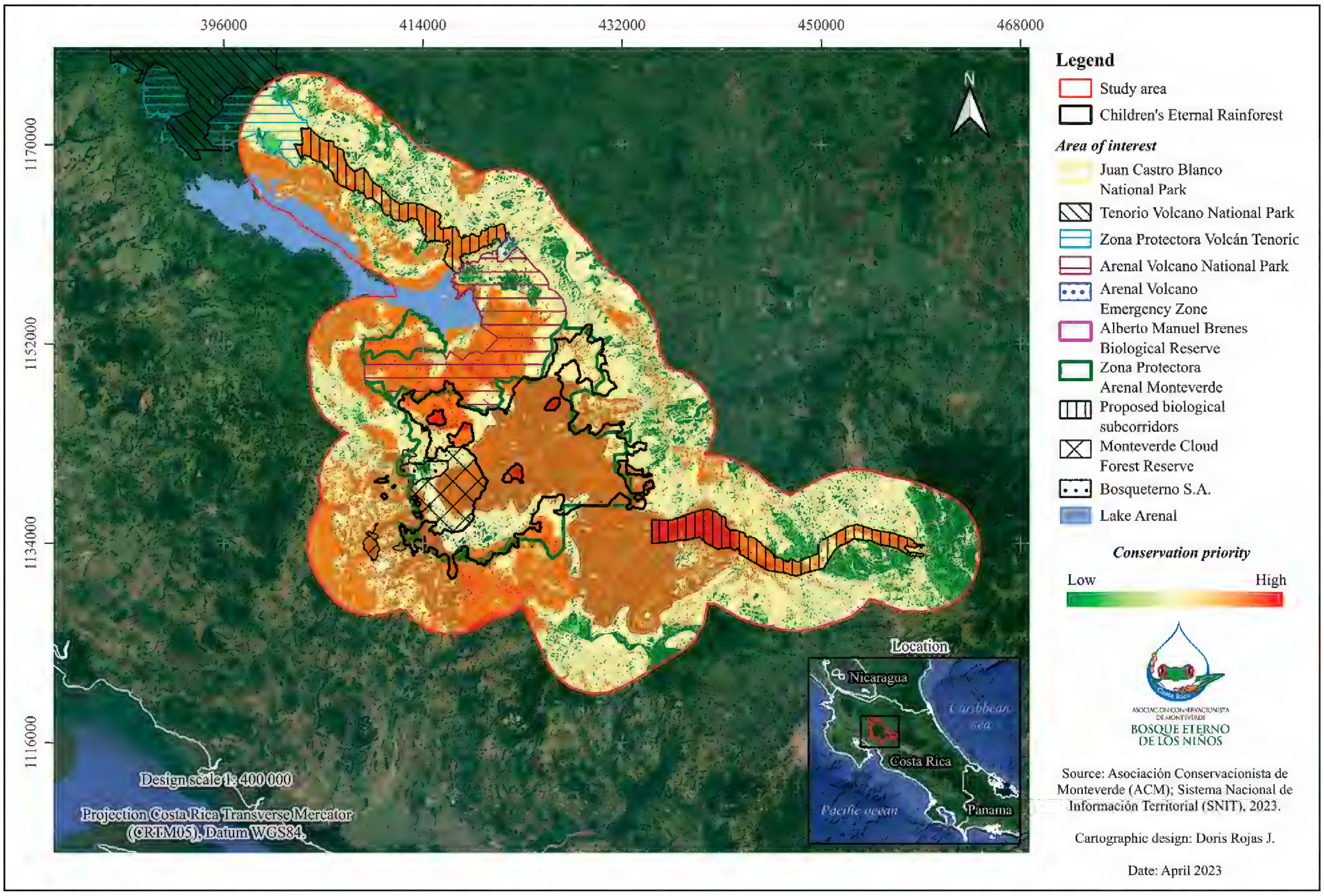

Figure 8. Conservation priority lands within the study area, based on all ecosystem services values included in the analysis.

protected areas and land connecting Arenal National Park with the Tenorio Complex to the northwest of Lake Arenal (Fig. 8). Land to the northeast of the existing protected areas is generally of lower conservation priority. The connectivity gap between the MAB and Juan Castro Blanco National Park is made up mostly of lower priority lands with fewer ecosystem services as compared to the gap between existing protected areas and the Tenorio Complex.

Discussion

Our analysis confirms the existence of unprotected lands with high conservation value in the vicinity of the existing protected areas of the MAB that should be the target of conservation activities. There are also areas that have comparatively less conservation value, showing that these types of analyses can help to prioritise the limited resources available for conservation. At this point in time, differentiating land more suitable for traditional economic activity from land that would be better utilised for protection of natural resources will be critical as societies try to balance economic needs with environmental and ecosystem services protection. This balance is even more critical for countries like Costa Rica, whose strong tourism (and especially ecotourism) sector outweighs benefits from extractive activities and depends on a healthy natural environment to sustain its economic well-being.

The first area which we identified as high priority for conservation includes lower elevations on the Pacific slope to the south and west of the existing protected areas in the MAB. This region has a high number of closely altitudinal-

ly-spaced life zones, several of which have high species diversity and endemism. The life zones in this area are also poorly protected in the study area (and in Costa Rica in general). As the climate in these life zones tends to be favourable for cattle ranching and coffee growing, much of this habitat was deforested many years ago for agricultural use. However, some forested areas remain, especially on steep slopes and in riparian zones. Additionally, these areas have experienced an increase in reforestation over the past few decades as the more marginal agricultural areas have been abandoned and allowed to regenerate (Chacón-Cascante et al. 2012).

The second priority area for future conservation efforts lies between Arenal National Park and the Tenorio Complex, to the northeast east of Lake Arenal. There are actually two potential corridors here: one along the sub-corridor proposed in Moran et al. (2019) and another along the northern shore of the Arenal reservoir. Both areas have relatively high forest cover and fall within this important watershed for Costa Rican electricity production. These areas are also sparsely populated (with the exception of La Fortuna and adjacent communities), with most deforested lands devoted to cattle ranching (MDM, personal observation) and almost no permanent crops or human settlements (Fig. 2D).

The establishment of biological sub-corridors that extend outwards from the existing protected areas of the MAB would conceivably be positive in supporting populations of animals that need large areas for viable populations (Weber and Rabinowitz 1996; Crooks and Sanjayan 2006; Hilty et al. 2012) and in helping some species survive the dispersal expected to be necessary to adjust to climate change (Heller and Zavaleta 2009; Fung et al. 2017; Beita et al. 2021). The Bellbird Biological Corridor was created in part to protect and improve habitat for altitudinal migrants, such as frugivorous birds and some Lepidoptera (Welch et al. 2011; Newcomer et al. 2022). As this analysis shows, land within and adjacent to this corridor also has high value for many other ecosystem services, such as high biodiversity and soil conservation on steep slopes. The proposed corridor between the MAB and the Tenorio Complex would help to connect the protected areas of the Cordillera de Tilarán (MAB) to protected areas in the Cordillera de Guanacaste (with numerous important protected areas), which apparently have healthy populations of Baird's tapirs (*Tapirus bairdii*, Carbonell and González-Zúñiga 2000) and jaguars (*Panthera onca*, Montalvo et al. 2022), two species imperiled in Costa Rica. These two species are present in the MAB, but only at low population densities (Zamzow et al. 2018) that are likely not viable in the long-term. With the larger populations of tapirs in the Tenorio Complex and jaguars across the Cordillera de Guanacaste into the tropical dry forests beyond (Calvo-Alvarado et al. 2009), a corridor connecting these areas to the MAB would likely increase probabilities of survival for these species across north-central Costa Rica.

A third potential area of focus, extending from the MAB to Juan Castro Blanco National Park, is more problematic. While the western part of the proposed sub-corridor has abundant forested lands of high conservation value (Fig. 4), the eastern portions comprise landscapes with comparatively low ecosystem services and include extensive areas of pasture and cultivated lands (ornamental plants are a large industry in this region). Creating a functional biological

corridor in this area would, therefore, likely be expensive and logistically difficult. Considering economic limitations for land acquisition and other conservation efforts, it would, therefore, be preferable to focus on the other two areas mentioned above (Bellbird and Arenal-Tenorio).

The entire region falls within the Mesoamerican Corridor proposal (Miller et al. 2001), which extends from Panama to Mexico, with the jaguar (*P. onca*) as its flagship species. Due to political instability and other social challenges throughout the region, the creation of a functional mega-corridor remains a logistical challenge. However, within Costa Rica, the completion of this corridor is more feasible, given the large amount of land currently under protection, the historically strong conservation efforts country-wide and the long-term political stability of the country. The opportunity to create benefits for the local economy by ecotourism may also foster the completion of the corridor in Costa Rica. There are only relatively small gaps between large protected areas, so that a small, carefully targeted increase in lands under conservation could potentially link all of Costa Rica's major protected areas across the entire length of the country. Ultimately, if Costa Rica hopes to preserve its rich biodiversity in perpetuity, this landscape-scale conservation strategy is probably the best method. Fortunately, with the already extensive system of public and private protected areas, along with focused efforts on remaining lands that retain high conservation values, there is a good probability that Costa Rica can continue to be a model for 21st century conservation.

Conclusions

This analysis shows that conservation efforts in the MAB have been successful in creating a large complex of biodiverse protected areas. Yet these areas remain an island of protected lands isolated from larger regional protected areas and several life zones remain completely unprotected. However, land of high conservation value and low traditional economic value remains that, if placed under conservation, could mitigate these two issues. Considering the incredibly high contribution of this area to Costa Rica's total biodiversity and the large ecotourism economy dependent upon this biodiversity, we urge conservation organisations to consider how to achieve expanded, but selective land conservation of the MAB, possibly through a combination of direct land purchase, ecotourism development in these areas and cooperative agreements between landowners and conservation organisations. Examples of direct land purchase priorities might include some of the highest conservation priority areas of the Bellbird Biological Corridor directly adjacent to protected areas and/or the smaller unforested areas of the Tenorio Corridor that would, if reforested, connect larger areas of forest together. However, since direct purchase of all high conservation priority lands is financially and logistically difficult, we expect that cooperative work with private landowners will be the primary way to achieve greater success in preserving the rich biodiversity of this region.

Acknowledgements

We wish to thank the Alex C. Walker Foundation for their generous funding for this project. Peter Gausmann and João Pompeu provided valuable feedback that improved this manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This work was supported by Alex C. Walker Foundation.

Author contributions

Conceptualization: LS, MDM. Data curation: EM, DR. Formal analysis: EM, MDM, DR, LS. Funding acquisition: MDM, LS. Investigation: LS. Methodology: LS, MDM. Project administration: LS. Software: EM, DR. Supervision: LS. Writing - original draft: MDM. Writing - review and editing: LS, EM, MDM, DR.

Author ORCIDs

Matthew D. Moran https://orcid.org/0000-0002-8611-6092

Data availability

All of the data that support the findings of this study are available in the main text.

References

Aylward B, Allen K, Echeverría J, Tosi J (1996) Sustainable ecotourism in Costa Rica: The Monteverde cloud forest preserve. Biodiversity and Conservation 5: 315–343. https://doi.org/10.1007/BF00051777

Beita CM, Murillo LFS, Alvarado LDA (2021) Ecological corridors in Costa Rica: An evaluation applying landscape structure, fragmentation-connectivity process, and climate adaptation. Conservation Science and Practice 3(8): e475. https://doi.org/10.1111/csp2.475

Brunbjerg AK, Bruun HH, Dalby L, Fløjgaard C, Frøslev TG, Høye TT, Goldberg I, Læssøe T, Hansen MD, Brøndum L, Skipper L, Fog K, Ejrnæs R (2018) Vascular plant species richness and bioindication predict multi-taxon species richness. Methods in Ecology and Evolution 9(12): 2372–2382. https://doi.org/10.1111/2041-210X.13087

Calvo-Alvarado J, McLennan B, Sánchez-Azofeifa A, Garvin T (2009) Deforestation and forest restoration in Guanacaste, Costa Rica: Putting conservation policies in context. Forest Ecology and Management 258(6): 931–940. https://doi.org/10.1016/j.foreco.2008.10.035

Cañadas EM, Fenu G, Peñas J, Lorite J, Mattana E, Bacchetta G (2014) Hotspots within hotspots: Endemic plant richness, environmental drivers, and implications for conservation. Biological Conservation 170: 282–291. https://doi.org/10.1016/j.biocon.2013.12.007

Carbonell F, González-Zúñiga J (2000) Análisis Ecológico para la Determinación del Hábitat Actual y Potencial del Tapir (*Tapirus bairdii*) en el Parque Nacional Volcán Tenorio y Zona Protectora Miravalles. ACA-SIG-INBIO. http://www.inbio.eas.ualberta.ca/es/estudios/PDF/Informe_Danta.pdf

Chacón-Cascante A, Ibrahim M, Ramos Z, De Clerk F, Vignola R, Robalino J (2012) Costa Rica: National level assessment of the role of economic instruments in the

conservation policymix. Policymix. http://repositorio.bibliotecaorton.catie.ac.cr/handle/11554/7741

Chang M (2006) Forest Hydrology: An Introduction to Water and Forests (2nd edn.). CRC Press, Boca Raton, FL, 488 pp.

Crooks KR, Sanjayan M (2006) Connectivity conservation (Vol. 14). Cambridge University Press, Cambridge, UK. https://doi.org/https://doi.org/10.1017/CBO9780511754821

Fung E, Imbach P, Corrales L, Vilchez S, Zamora N, Argotty F, Hannah L, Ramos Z (2017) Mapping conservation priorities and connectivity pathways under climate change for tropical ecosystems. Climatic Change 141(1): 77–92. https://doi.org/10.1007/s10584-016-1789-8

Haber WA (2000) Plants and vegetation. In: Nadkarni NM, Wheelwright NT (Eds) Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford University Press, New York, NY, 39–94. https://doi.org/10.1093/oso/9780195095609.003.0009

Harvey CA, Komar O, Chazdon R, Ferguson BG, Finegan B, Griffith DM, Martínez-Ramos M, Morales H, Nigh R, Soto-Pinto L, Van Breugel M, Wishnie M (2008) Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. Conservation Biology 22(1): 8–15. https://doi.org/10.1111/j.1523-1739.2007.00863.x

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142(1): 14–32. https://doi.org/10.1016/j.biocon.2008.10.006

Hilty JA, Lidicker WZ, Merenlender AM (2012) Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation. Island Press, Washington, DC, USA.

Holdridge LR (1947) Determination of world plant formations from simple climatic data. Science 105(2727): 367–368. https://doi.org/10.1126/science.105.2727.367

Holdridge LR (1967) Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

Holland MB (2012) Mesoamerican biological corridor. Climate and conservation: Landscape and seascape science, planning, and action. In: Hilty JA, Chester CC, Cross MS (Eds) Climate and Conservation. Island Press/Center for Resource Economics. Washington DC, USA, 56–66. https://doi.org/https://doi.org/10.5822/978-1-61091-203-7_5

Janzen DH, Hallwachs W (2020) Área de Conservación Guanacaste, northwestern Costa Rica: Converting a tropical national park to conservation via biodevelopment. Biotropica 53(6): 1017–1029. https://doi.org/10.1111/btp.12755

Jiménez-López DA, Gallardo-Cruz JA, Véliz ME, Martínez-Camilo R, Méndez C, Solórzano JV, Velázquez-Méndez L, Carabias J, García-Hidalgo G, Peralta-Carreta C, Sánchez-González M, Castillo-Acosta O, Luna-Kamyshev NM, Villaseñor JL, Meave JA (2023) High vascular plant species richness in the Usumacinta River Basin: A comprehensive floristic checklist for a natural region in the Mesoamerican biodiversity hotspot. Botanical Sciences 101(3): 908–930. https://doi.org/10.17129/botsci.3253

Kjekstad O, Highland L (2009) Economic and Social Impacts of Landslides. In: Sassa K, Canuti P (Eds) Landslides – Disaster Risk Reduction. Springer, Berlin, Heidelberg, 573–587. https://doi.org/https://doi.org/10.1007/978-3-540-69970-5_30

Koens JF, Dieperink C, Miranda M (2009) Ecotourism as a development strategy: Experiences from Costa Rica. Environment, Development and Sustainability 11(6): 1225–1237. https://doi.org/10.1007/s10668-009-9214-3

Kohlmann B (2011) Biodiversity Conservation in Costa Rica - An Animal and Plant Biodiversity Atlas. In: Pavlinov I (Ed.) Research in Biodiversity - Models and Applications. INTECH Open Access Publisher, Croatia, 203–222. http://doi:https://doi.org/10.5772/24546

Langholz JA, Lassoie JP, Lee D, Chapman D (2000) Economic considerations of privately owned parks. Ecological Economics 33(2): 173–183. https://doi.org/10.1016/S0921-8009(99)00141-X

Lehmann P, von Ruette J, Or D (2019) Deforestation effects on rainfall-induced shallow landslides: Remote sensing and physically-based modelling. Water Resources Research 55(11): 9962–9976. https://doi.org/10.1029/2019WR025233

Miller K, Chang E, Johnson N (2001) Defining common ground for the Mesoamerican Biological Corridor. World Resources Institute, Washington, DC, 5 pp. http://www.bio-nica.info/Biblioteca/Miller2001.pdf

Montalvo VH, Sáenz-Bolaños C, Cruz-Díaz JC, Carillo E, Fuller TK (2022) The use of camera traps and auxiliary satellite telemetry to estimate jaguar population density in northwestern Costa Rica. Animals 12(19): 2544. https://doi.org/10.3390/ani12192544

Moran MD, Monroe A, Stallcup L (2019) A proposal for practical and effective biological corridors to connect protected areas in northwest Costa Rica. Nature Conservation 36: 113–137. http://doihttps://doi.org/10.3897/natureconservation.36.27430

Newcomer Q, Camacho Céspedes F, Stallcup L (2022) The Monteverde Cloud Forest: evolution of a biodiversity island in Costa Rica. In: Montagnini F (Ed.) Biodiversity Islands: Strategies for Conservation in Human-Dominated Environments. Cham: Springer International Publishing, New York, NY, USA, 237–278. https://doi.org/10.1007/978-3-030-92234-4_10

Our World of Data (2023) Our World of Data. https://ourworldindata.org/energy/country/costa-rica#what-sources-does-the-country-get-its-energy-from

Pounds JA, Fogden MP (2000) Appendix 8: amphibians and reptiles of Monteverde. In: Nadkarni NM, Wheelwright NT (Eds) Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford University Press, New York, 537–538.

Sánchez-Azofeifa GA, Daily GC, Pfaff AS, Busch C (2003) Integrity and isolation of Costa Rica's national parks and biological reserves: Examining the dynamics of land-cover change. Biological Conservation 109(1): 123–135. https://doi.org/10.1016/S0006-3207(02)00145-3

SNIT (National Territorial Informational System) (2023) Instituto Geográfico Nacional, San Jose, Costa Rica. https://www.snitcr.go.cr/

Stan K, Sanchez-Azofeifa A (2019) Deforestation and secondary growth in Costa Rica along the path of development. Regional Environmental Change 19(2): 587–597. https://doi.org/10.1007/s10113-018-1432-5

Stuckey JD, Camacho FC, Vargas GL, Stuckey SA, Vargas JL (2014) Agriculture in Monteverde, Moving Toward Sustainability. In: Nadkarni NM, Wheelwright NT (Eds) Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford University Press, New York, 389–417.

TEEB (2010) Mainstreaming the Economics of Nature: A Synthesis of the Approach, 787 Conclusions and Recommendations of TEEB. Earthscan, London, UK and 788 Washington, DC, 33 pp.

Teske S, Morris T, Nagrath K (2020) 100% Renewable Energy for Costa Rica. Report prepared by ISF for the World Future Council/Germany and the One Earth Foundation, USA, 77 pp. https://www.worldfuturecouncil.org/wp-content/uploads/2019/12/Costa_Rica-Report-2019-12-11-Excl_employ-1.pdf

Waylen PR, Quesada ME, Caviedes CN (1996) Temporal and spatial variability of annual precipitation in Costa Rica and the Southern Oscillation. International Journal of Climatology 16(2): 173–193. https://doi.org/10.1002/(SICI)1097-0088(199602)16:2<173::AID-JOC12>3.0.CO;2-R

Weber W, Rabinowitz A (1996) A global perspective on large carnivore conservation. Conservation Biology 10(4): 1046–1054. https://doi.org/10.1046/j.1523-1739.1996.10041046.x

Welch J, Chavarrìa A, Crespo R, Bolaños Barrantes J, Brenes Morera W, Feoli Boraschi S B. Gómez AB, Bolaños Cerdas V, Carvajal Barrientos S, Lorena Vargas A, Camacho Céspedes F, Guevara Villegas A, Villegas Villegas E, Aguilar G, Elena Mora M, Valverde Alpizar O, Debra Hamilton D, Méndez Y, Días Fonseca M, Bello Villalobos W, Segura Méndez R, Sofía Arce F, Castillo Mora A, Molina Arroyo K, Mata E, Vargas N, Newcomer Q, Irwin K, Nibbelinck N, Shelton J, Connelly S, Malloy R, Oduber Rivera J (2011) Plan Estratégico del Corredor Biológico Pájaro Campana (CBPC) 2011–2016. Monteverde, Costa Rica. https://www.uvm.edu/~lkutner/CBPC%20Plan%20Estrategico%202011%20lk.pdf

Wheelwright N (2000) Conservation Biology. In: Nadkarni NM, Wheelwright NT (Eds) Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford University Press, New York, 419–456. https://doi.org/10.1093/oso/9780195095609.003.0018

Wheelwright N (2014) Conservation biology – update 2014. In: Nadkarni NM, Wheelwright NT (Eds) Monteverde: Ecology and Conservation of a Tropical Cloud Forest – 2014 updated chapters. Oxford University Press, New York.

Zamzow BK, Nieman SJ, Davis CN, Garro Cruz M, Monroe A, Stallcup L, Moran MD (2018) Status of large terrestrial vertebrates in the Monteverde-Arenal bioregion, northwestern Costa Rica. Tropical Conservation Science 11: 1940082918809617. https://doi.org/10.1177/1940082918809617